Camouflage

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Abstract

Animal camouflage has long been used to illustrate the power of natural selection, and provides an excellent testbed for investigating the trade-offs affecting the adaptive value of colour. However, the contemporary study of camouflage extends beyond evolutionary biology, co-opting knowledge, theory and methods from sensory biology, perceptual and cognitive psychology, computational neuroscience and engineering. This is because camouflage is an adaptation to the perception and cognition of the species (one or more) from which concealment is sought. I review the different ways in which camouflage manipulates and deceives perceptual and cognitive mechanisms, identifying how, and where in the sequence of signal processing, strategies such as transparency, background matching, disruptive coloration, distraction marks, countershading and masquerade have their effects. As such, understanding how camouflage evolves and functions not only requires an understanding of animal sensation and cognition, it sheds light on perception in other species.

Keywords: camouflage, defensive coloration, animal coloration, crypsis, visual perception

Introduction

'The colours of many animals seem adapted to their purposes of concealing themselves, either to avoid danger, or to spring upon their prey' (Darwin, 1794)

Writing some 15 years before his grandson Charles was even born, Erasmus Darwin was using animal camouflage to illustrate apparent design in nature. Over two centuries later, the peppered moth *Biston betularia* remains the textbook example of rapid evolution, driven by changes in the effectiveness of camouflage against altered backgrounds (Grant, 2012; Cook & Saccher, 2013). However, recent years have seen a change in the focus of research on camouflage, towards a dissection of the multiple mechanisms at play. The latter has been slow in coming, partly because the principles seem obvious (look like the background or something irrelevant), and partly because the necessary theory and tools for investigation lie outside evolutionary biology, in perceptual psychology and computational neuroscience. However, part of the explanation may lie in the brilliance of Hugh Cott.

Hugh Bamford Cott (1900 – 1987) was a British zoologist whose early career, military service aside, had a rather Darwinian flavour: theology at Cambridge, expedition to South America, a love of natural history, and a desire to explain apparent design in nature. He held lectureships at the Universities of Bristol and Glasgow and, subsequently, the post of Curator of Birds at the University of Cambridge's Museum of Zoology (Forsyth, 2014; Zoology Chronicles of the Cambridge University Museum, 2018). In 1940 he published the book "Adaptive Coloration in Animals", which consolidated and built upon the earlier work of the

pioneers of animal camouflage theory, most notably the entomologist Edward Bagnall Poulton and the painter Abbott Thayer (Poulton, 1890; Thayer, 1896, 1909, 1918). Cott's book was so perceptive, comprehensive, and persuasive (in large part helped by his fine illustrations), that one might have considered animal, and military, camouflage "solved". As Forsyth (2014), in her analysis of Cott's methods, says "his research is presented as a completed and sealed area of scientific study". His authority was enhanced by his advisory role in the development and deployment of military camouflage, working as a camouflage instructor for the British Army in World War II (Forsyth, 2014). "Cott's Adaptive Coloration in Animals must be the only compendious zoology tract ever to be packed in a soldier's kitbag" (Forbes, 2009, p.153). Yet, following WWII, military research on camouflage moved away from the early inspirations of biology and art, towards physics and engineering, signal masking outside the human-visible spectrum often being the pressing concern. In the latter part of the 20th century, the interesting colours for evolutionary and behavioural biologists were sexually selected and conspicuous; after all, Cott had shown that camouflage was understood. However, what Cott's book lacked was experimental evidence that the mechanisms he advocated actually worked, and in the way proposed. Furthermore, although he had the artist's intuitive understanding of how shading and tone can deceive the viewer, an understanding of perception rooted in neuroscience had, in 1940, yet to emerge. These gaps are what the last 20 years of research have filled, and which this article reviews: how camouflage exploits the mechanisms of perception and cognition. In particular, I will embed classical accounts of camouflage, and the different methods by which it is achieved, within a more recent perceptual framework of minimising the signal-to-noise ratio.

Exploiting receiver psychology

Knowledge of the perception and cognition of the seeker is necessary to understand the concealment strategies of the animal in hiding. But equally, an understanding of concealment strategies shed light on perception and cognition. The latter was realised by the Gestalt psychologists at the start of the 20th century, who used animal camouflage as evidence for the generality of their 'principles of grouping', the means by which the brain organises separate, simple, visual stimuli into discrete, coherent, objects (Osorio & Cuthill, 2015; Wagemans, 2018). For example, the fact that a prey species has contrasting colour patterns that intersect the edge of its body suggests that its predator's visual system uses similarity of colour and continuity of outline to detect and recognise prey (see Concealing Form). Indeed, Wolfgang Metzger, a key figure in the growth of the Gestalt school, said in his *Gesetze des Sehens* (Laws of Seeing) *"There is hardly a law of vision that is not found again serving camouflage*" (p.85, Metzger, 1936, transl. Spillman 2009).

The Gestalt principles generalise to other sensory modalities but were, and are, most often explained with reference to vision. So too with camouflage, as the bulk of the theory and examples relate to coloration; but non-visual camouflage follows the same principles (Ruxton, 2009). Two principles are essential to understanding camouflage: (i) whichever mechanism is employed, it acts to reduce the signal-to-noise ratio (Merilaita, Scott-Samuel & Cuthill, 2017), and (ii) both signal and noise are filtered in species-specific ways (Endler, 1978, 1990; Endler *et al.*, 2005).

The ‘signal’ is the object of interest and the ‘noise’ is anything else, so the conceptual framework is one of accurate classification. Whether a prey to be consumed or a predator to be avoided, the same principle of discrimination between relevant and non-relevant stimuli can be applied at any stage in information-processing (Merilaita, Scott-Samuel & Cuthill, 2017). Reduction of signal-to-noise ratio relates to the pattern of stimulation of neurones in a visual system, not the pattern of light, because signal and noise are filtered in species-specific ways. That humans are frequently deceived by animal camouflage is interesting, as this points to deep similarities in sensory processing between humans and other animals, but is ultimately irrelevant to an evolutionary understanding, because what matters is the perception of the receivers that exerted the selection pressure on the trait (Endler, 1978, 1987; Bennett, Cuthill & Norris, 1994). Studies of the physical properties of the signal and noise (in the case of coloration, the distribution of the reflected light in wavelength, time and space) are also tangential to understanding how camouflage works; what matters is psychophysics, not physics. This is because there is a massive reduction in the quantity of data between the physical signal and its encoding by a brain, and it is these perceptual ‘shortcuts’ that camouflage can exploit (Troscianko *et al.*, 2009; Merilaita, Scott-Samuel & Cuthill, 2017). There are three principle bottlenecks: in the eye, at the optic nerve and, finally, through attention. It is clear from the latter constraint that any account of how camouflage works must take into account cognition and not simply sensory processing (Skelhorn & Rowe, 2016).

Although the light from a visual scene is effectively continuous in its distribution, retinal processing results in information losses in space, time and spectral

composition. Wavelengths are lost through absorption by optical media (e.g. blocking of ultraviolet by the lens of some species, including humans; Douglas & Jeffery, 2014), the spectral resolution is limited by the number of photoreceptors in opponency (usually two to four; Kelber, Vorobyev & Osorio, 2003), the spatial resolution limit is related to the density of photoreceptors and their associated ganglion cells (Snyder & Miller, 1977; Woog & Legras, 2018) and, analogously, temporal resolution by the sampling frequency in time (Laughlin & Weckstrom, 1993; Warrant, 1999). A consequence for camouflage is that, for example, to match the colour of the background an animal need not match the reflectance spectrum of the background, only the pattern of stimulation of the viewer's (very) limited number of classes of broadband photoreceptors (Endler, 1978, 1987, 2012; Endler & Mielke, 2005; Endler *et al.*, 2005). Furthermore, that match need only be accurate at the spatial frequency the viewer is sampling at; in other words, as limited by their visual acuity (Caves, Brandley & Johnsen, 2018). This allows the same pattern to function as camouflage at a distance, but a signal when the intended viewer is close (Endler, 1978, 2012; Merilaita & Tullberg, 2005; Bohlin, Tullberg & Merilaita, 2008; Barnett & Cuthill, 2014; Barnett *et al.*, 2016, 2018; Barnett, Scott-Samuel & Cuthill, 2016; Barnett, Cuthill & Scott-Samuel, 2017, 2018).

The second major loss of information occurs at the optic nerve. For example, the human retina has around 5 million cones and 90 million rods (Curcio *et al.*, 1990), but the optic nerve has only 1.5 million neurons (Jonas *et al.*, 1992), so pixel-by-pixel transfer of information, as in a digital camera, is clearly not occurring. The nature of the data compression again has consequences for camouflage. For example, because the boundaries of objects are detected as a rapid change in light intensity or

hue over space, artificially enhancing the contrast between two colours within a single surface creates a powerful false edge that disguises the true shape (see Concealing Form: Disruptive Coloration).

The bottleneck at the point of visual attention is even greater with, in humans, 100 bits s^{-1} being processed compared to the 10^7 bits s^{-1} coming through the optic nerve, a 10,000-fold drop in information content (Zhaoping, 2014). While it is clear that attention allows an enhanced signal-to-noise ratio, achieved through orientation, selective use of information and integration of features otherwise processed in parallel (Carrasco, 2011, 2018), necessarily the signal-to-noise ratio is poorer away from the focus of attention, and so this can be exploited. Successful camouflage is as much about escaping the focus of attention as it is about remaining below the threshold for detection or recognition when all perceptual and cognitive resources are brought to bear on the target (Skelhorn & Rowe, 2016). Limited attention can also be exploited by group-living species. If individuals are all of similar appearance and motion, it is harder for a predator, because of limited attention, to target and track an individual prey; the so called ‘confusion effect’ (Landeau & Terborgh, 1986; Krakauer, 1995; Scott-Samuel *et al.*, 2015). Coloration can enhance the confusion effect, making it harder to track or discriminate one target from others (Hall *et al.*, 2013, 2017; Hogan, Cuthill & Scott-Samuel, 2016, 2017; Hogan, Scott-Samuel & Cuthill, 2016).

Peeling the onion

A common military framework for understanding defensive strategies is the 'survivability onion' (Figure 1). Usually in the context of avoiding a lethal strike on a vehicle, the imperatives are, in order, don't be: there, detected, identified, acquired, engaged, hit, penetrated, or affected. These have direct biological analogues for a potential prey (c.f. Edmunds, 1974; Lima & Dill, 1990). Safest is to avoid danger in the first place, through habitat choice or vigilance and moving away. If proximity to the predator cannot be avoided, then concealment through hiding or crypsis ('hiding in plain sight') is the next option. If detection is inevitable, then avoiding recognition, or promoting misidentification, is the next line of defence. If correctly identified, then strategies to avoid selection ('target acquisition') and attack ('engagement') can be employed, including pursuit-deterrence signals (Caro, 2005) and, more generally, advertisement of elusiveness (Ruxton *et al.*, 2018). Aposematism, the signalling of unprofitability, falls within this 'layer of the onion' and, although usually thought of as an alternative to the previous types of defence, can be facultative (Skelhorn, Holmes & Rowe, 2016; Umbers & Mappes, 2016) or distance-dependent (Bohlin, Tullberg & Merilaita, 2008; Barnett & Cuthill, 2014), so only employed when crypsis has failed. If the predator does attack, then a startle or 'deimatic' display can give time for escape, through targeting the predator's reflex protective behaviour in response to unexpected stimuli (Skelhorn, Holmes & Rowe, 2016; Umbers & Mappes, 2016). Otherwise, unpredictable ('protean') escape patterns can make capture difficult (Humphries & Driver, 1970; Scott-Samuel *et al.*, 2015). The final layers of the onion are avoidance of being killed or seriously injured; here, deflection marks can misdirect to less important body parts (Kjernsmo & Merilaita, 2013; Fresnillo, Belliure & Cuervo, 2015; Prudic *et al.*, 2015).

Camouflage, as understood today, operates in the outer layers of the survivability onion. It has not always been thus, with patterns that act to confuse or misdirect attacks included within the same framework. For example, ‘dazzle camouflage’ (*sic*), high contrast geometric patterns used on ships, particularly in World War I, was designed to undermine targeting by submarine commanders (Behrens, 1988, 2012; Hartcup, 2008; Bekers, Meyer & Strobbe, 2016). While some designs contained elements of disruptive patterning and masquerade (e.g. mimicking already sunk ships; see examples in Behrens, 2012), the more abstract geometric patterns were designed to interfere with range, speed and direction estimation (Behrens, 2012; Bekers, Meyer & Strobbe, 2016). While there is no good evidence for, or against, such patterns reducing shipping losses in wartime, or protecting animals in the wild, there is evidence for the proposed effects in laboratory experiments on humans (Stevens, Yule & Ruxton, 2008; Scott-Samuel *et al.*, 2011; Hughes, Troscianko & Stevens, 2014). While these effects of coloration certainly count as deception through manipulation of perception, and the word camouflage is derived from the French colloquialism *camoufler*, to deceive, contemporary usage limits camouflage to strategies for avoidance of detection and recognition (Stevens & Merilaita, 2011; Ruxton *et al.*, 2018).

Most historical and contemporary accounts of animal camouflage have the primary sub-types of background matching, disruptive coloration and masquerade, with transparency and countershading included under one of these headings or discussed separately. Instead, Merilaita *et al.* (2017) analyse the sequence of perceptual mechanisms from near-retina encoding of simple features through to object recognition, specifying how different camouflage mechanisms act to reduce

the signal or increase the noise from which that signal must be separated (see also Troscianko *et al.*, 2009). Here I use a hybrid approach, discussing the classical camouflage lexicon within a perceptual framework. For example, an animal with background matching camouflage reproduces the same distribution of simple features as found in the background, so no information that could contribute to discrimination is even passed on for further processing. Other types of camouflage act at a later stage in perception, acting to inhibit the grouping of simple features into 'things' that possess form or other collective attributes which could potentially be recognised. Disruptive coloration has this effect, and countershading can reduce information about 3D shape. Finally, masquerade has its effect after perceptual segregation of an object, though misclassification as something irrelevant. The mapping between the classical and perceptual breakdown is not perfect, as some types of coloration can have effects at more than one stage in perceptual processing but, as we shall see, it is useful to identify where those effects act.

Transparency and mirrors

The invisibility cloaks of fiction and, thanks to a branch of physics known as transformation optics, ever-closer to science fact (McCall *et al.*, 2018), are not found in nature, but many organisms are transparent. Allowing light from the background to pass through you would seem to be the ideal camouflage, because concealment is not background or behaviour dependent; you match the background because what the viewer sees is the background. That the majority of wholly transparent organisms are pelagic, living in mid-water, is the first clue to the constraints on this camouflage strategy (Johnsen, 2001). Unless the medium around the organism has a very

similar refractive index to its tissues – true of water but not air – some light will be reflected and refracted at the interface between the two (Johnsen, 2011). Invisibility requires no effect on the transmitted light, so a lack of absorption or scattering is not enough. Furthermore, the same constraints apply to any tissues within the body: they must be of the same refractive index, and any organelles or other structures that might scatter light need to be at low density. Some biological tissues have oriented structures for mechanical reasons (e.g. muscle, cuticular proteins) and this polarises incident light. Because many invertebrates and fish are sensitive to the polarisation of light, some with moderately high acuity (Temple *et al.*, 2012), a polarisation contrast with the backdrop of open water can be detected (Shashar, Hanlon & Petz, 1998; Shashar *et al.*, 2000; Flamarique & Browman, 2001; Pignatelli *et al.*, 2011; Cartron *et al.*, 2013). Non-polarising tissue of the same refractive index as water, and with few light-wavelength-sized structures, is the obvious countermeasure. Being made of jelly works, and may be compatible with the lifestyle of a jellyfish, but the constraints are significant (and even a jellyfish is not invisible). That said, in a featureless environment where physically hiding is impossible, and scattering by the medium itself both introduces veiling light (increasing noise) and limits transmission range (reducing signal), even partial transparency can be advantageous (Ruxton *et al.*, 2018).

A different solution, with analogous effects, is the use of mirrors, and the silvering of many pelagic fish is an oft-quoted example (McFall-Ngai, 1990; Herring, 1994). For a mirror to work as camouflage, what it reflects, which lies in front, has to match what is behind. In the featureless environment of mid-water, this would seem plausible. However, the assumption that the light field is symmetrical underwater does not hold

under many conditions and so the robustness of silvering-as-camouflage has been called into doubt (Johnsen *et al.*, 2014). Mirrored scales have other potential defensive functions: perhaps, when the fish turns, a startle effect (Umbers & Mappes, 2016) or the sudden change in appearance interferes with target tracking (Loeffler-Henry *et al.*, 2018). None of these possibilities, or the putative concealing effects originally assumed for mirrored scales, has been tested *in situ*. So, whether silvering acts as camouflage is as yet unproven (Johnsen *et al.*, 2014).

Background matching

If one were able to ask Erasmus Darwin what observation had led him to the statement quoted at the start of this review, he'd probably say that animals are often the same colour as their backgrounds and this makes them hard to see. Bearing the same colours and patterns as the background is most people's conception of camouflage, captured in Thayer's term "background picturing" (Thayer, 1909) or, more commonly today, "background matching" (Endler, 1984; Merilaita & Stevens, 2011). The American artist Abbott Thayer, who has been described as the "Father of Camouflage" (Behrens, 1988), saw all animal colours as samples of those in the background (Fig. 2). He supported this proposition by comparing paintings of backgrounds through animal-shaped stencils to the real animals' colours (Thayer, 1909, 1918; Behrens, 2018).

A correlation between the coloration of species and the habitats they live in is suggestive of the prevalence of background matching as an anti-predator strategy. For example, Endler (1984) showed that the distribution of colour patches on different species of moths was correlated with those of the background at the time of

the year that they were active. Similarly, Allen *et al.* (2011) used a quantitative description of felid coat pattern development to show that cat species from open habitats, particularly mountains, tend to have plain coats, while those in closed habitats, such as tropical forests, more often have complex and irregular patterns. This confirms conclusions from more subjective classifications of patterning (Ortolani & Caro, 1996) and is consistent with forests having more complex physical structure, and illumination patterns (Endler, 1993), than plains or rocky slopes. However, such correlations can only ever be the starting point for camouflage research, because the same correlation could be be the result of contemporary selection (the conspicuous individuals have been eaten) rather than being evidence of adaptation through past selection (see the discussion of alternative explanations for phenotype-background correlations in Stevens *et al.*, 2015). So, more convincing evidence for the importance of background matching comes from relating survival to the match between animal and background. Troscianko *et al.* (2016) did exactly this, showing that clutches of ground-nesting plovers (Charadriidae) and coursers (Glareolidae) were predated less often when their eggs matched their local background. Conversely in nightjars (Caprimulgidae), which do not flee the nest when a predator approaches and instead sit tight on the eggs, it was the match of the adult's plumage pattern that predicted survival (Fig. 3). Colour change (Umbers *et al.*, 2014; Duarte, Flores & Stevens, 2017), substrate selection in relation to phenotype (e.g. Kang *et al.*, 2012; Kjernsmo & Merilaita, 2012; Lovell *et al.*, 2013; Marshall, Philpot & Stevens, 2016; Smithers *et al.*, 2018), and orientation behaviour to match the orientation of substrate textures (Kang *et al.*, 2012, 2014a, 2014b), are also powerful evidence for the importance of background matching for concealment (see review by Stevens & Ruxton, 2019).

That variation in patterning or coloration affects detectability, or a more direct fitness measure, is a critical metric for camouflage, but it does not by itself reveal what aspect of a pattern makes it successful or, indeed, whether it is optimal. The first issue is what measure of 'background matching' to use. Colour would appear 'easy' in the sense that there are measurements (e.g. Goldsmith & Butler, 2005; Lind & Kelber, 2009b) and models of threshold colour discrimination (Vorobyev & Osorio, 1998; Vorobyev *et al.*, 2001; Kelber, Vorobyev & Osorio, 2003). There are caveats in that these models have only been validated for large objects under ideal conditions in the laboratory (Vorobyev & Osorio, 1998; Goldsmith & Butler, 2003; Lind & Kelber, 2009a), but the conceptual model of colour differences being related to distance in a 'colour space', with axes determined by the neural opponent processing of photoreceptor excitations, is well established. A greater problem is how to quantify the match between any two patterns (or 'visual textures'), there being no single agreed representation, even for humans, analogous to a colour space (Osorio & Cuthill, 2015). A good approach is to analyse the overlap (in a species-specific colour space) of the distributions of all colours in the objects being compared (Endler & Mielke, 2005), or the size distribution and spatial adjacency of colour patches (Endler, 1984, 2012). Better still, from the perspective taken in this review, is to decompose the patterns with respect to their different spatial frequency components, which can then be used to assess similarity at coarse- to fine-grained detail, or to produce an aggregate measure of 'match' (the method used by Troscianko *et al.*, 2016; Wilson-Aggarwal *et al.*, 2016). This is an appealing approach because this is similar to what happens in the initial stages of visual processing (Troscianko *et al.*, 2009; Osorio & Cuthill, 2015; Merilaita, Scott-Samuel & Cuthill, 2017). The

distribution of the power and phase of the different spatial frequencies at different orientations is therefore a high-dimensional, but tractable and physiologically plausible, representation of the raw pattern information (Michalis *et al.*, 2017; Talas, Baddeley & Cuthill, 2017).

Armed with such methods, one can also ask what the optimal background-matching camouflage should be. At any one location (e.g. resting spot), the answer is easy to state – it is the pattern that the viewer would predict to be there in the absence of the occluding object in question. No further inspection is provoked if the viewer sees "an average and most expectable type of scene" (Thayer, 1918, p.494). Substrate selection or colour change helps achieve that match but, if such fine-tuning isn't possible, which of the many possible background samples, or combinations thereof, would be globally optimal? Endler (1978, 1981, 1984) has been criticised for suggesting that a random sample might be best (Merilaita, Tuomi & Jormalainen, 1999), the problem being that random samples include rare samples which may be poor matches to the actual local background where the animal is resting (Michalis *et al.*, 2017). However, the context of statements such as "Cryptic prey resemble random samples of the visual background" (Endler, 2006) was to distinguish generalised background resemblance from mimicry of specific background objects (masquerade). Michalis *et al.* (2017), in field experiments where both humans and avian predators searched for background-matching artificial prey, showed that the best single camouflage pattern was that of the most likely background sample (where 'likely' was quantified using colour and texture modelling of the kind described earlier).

Michalis *et al.* (2017) were investigating the situation of a variable, but single type of, background, and infrequent encounters by the predator relative to other prey types. They pointed out that, conversely, if predators learnt the characteristics of a specific pattern through repeated encounters, then negative frequency-dependent selection would favour polymorphism. A learnt conjunction of features in an otherwise cryptic prey, resulting in a short-term perceptual filter through selective attention, is what biologists describe as a 'search image' (Allen, 1989; Langley, 1996). The fact that search image formation improves detection of frequently encountered prey at the expense of reduced detection of infrequent prey (Pietrewicz & Kamil, 1979; Reid & Shettleworth, 1992; Plaisted & Mackintosh, 1995) does indeed favour polymorphism in prey appearance (Bond & Kamil, 2002; Karpestam, Merilaita & Forsman, 2014). That said, because some types of camouflage pattern seem to be easier to learn than others (Troscianko *et al.*, 2013; Troscianko, Skelhorn & Stevens, 2018), the polymorphism may be constrained in ways that are as yet not fully understood.

If an animal needs concealment against multiple backgrounds, then the benefits of matching one background are traded off against greater conspicuousness on others. If the latter costs don't outweigh the former benefits then a compromise camouflage that fares reasonably well on several backgrounds can be favoured (Merilaita, Tuomi & Jormalainen, 1999; Houston, Stevens & Cuthill, 2007). Although aviary experiments with birds searching for artificial prey show that compromise camouflage can work (Merilaita, Lyytinen & Mappes, 2001), identifying whether any real animal's coloration represents such an adaptive compromise is a challenge. This is because all the backgrounds against which the animal might be seen need to

be characterised, along with their risk of detection on those backgrounds (see discussion in Ruxton *et al.*, 2018, pp. 17-21).

Concealing form

Although Thayer argued that background picturing could be as effective as complete transparency (Behrens, 2018), he also pointed to its limitations (Thayer, 1909). Unless the background has a homogeneous texture (at the spatial scale of the animal; Endler, 1978), or the animal aligns itself carefully with the background, there may be mismatches between patches on the animal and patches in the background. This may make its outline discernible, or create patch shapes -- on the animal or, via occlusion, the background -- that are unusual (Cuthill & Troscianko, 2009). There may also be a cast shadow, or differential shading on the animal's body, that highlights the body's edge. Shape, as revealed by an outline or pattern of shading, is a powerful cue to identity, in most cases more so than surface coloration *per se*. Thayer (1909) proposed three mechanisms that could directly interfere with the perception of form -- disruption, distraction and countershading – although the distinction between the first two was not always clear in his writings. Instead, Cott's (1940) accounts are lucid, and modern evidence supports most of his arguments.

Disruptive coloration

Cott defined disruptive coloration as "a superimposed pattern of contrasted colours and tones serving to blur the outline and to break up the real surface form, which is replaced by an apparent but unreal configuration" (Cott, 1940, p.4). Much of his subsequent discussion invoked distraction of attention but, now that we have a better understanding of visual perception, we can see that the key components (also, or

exclusively) have pre-attentive effects. The first ingredient is what Cott called ‘differential blending’: some of the colours of the animal match those in the background well. This much is the same as background matching, the similarity in colour and texture of some colour patches reducing the signal at the body’s edge that might reveal a transition from background to target. The next ingredient is ‘maximum disruptive contrast’: directly adjacent to the background-matching colours are colour patches with highly contrasting tones or hues (Fig. 2). Rather than reducing the signal, this enhances noise by creating false edges which are more salient than the animal’s real outline (Stevens & Cuthill, 2006; Troscianko *et al.*, 2009). Also, as illustrated by Cott himself with pictures of snakes (Cott, 1940, p.58), the boundaries are sometimes optically enhanced by, where the patches meet, the tone becoming lighter on the light side and darker on the dark side (Fig. 2; Osorio & Srinivasan, 1991). Visual search experiments with humans shows that such edge enhancement is highly effective (Egan *et al.*, 2016). It is the salience of the false edges and the contrasting surfaces within those boundaries that creates the “apparent but unreal configuration” which Cott referred to. The shapes are salient but apparently unconnected, and thus perceptual grouping of simple features into potentially recognisable forms is defeated (Espinosa & Cuthill, 2014). Experiments with humans searching for animal shapes indicate that edge enhancement interferes with object recognition, not only detection (Sharman, Moncrieff & Lovell, 2018). If the contrasting colour patches intersect the body’s edge, the continuity of the signal at the true outline is reduced, and this form of disruptive coloration has been shown to be more effective against both birds and humans than background matching alone (Cuthill *et al.*, 2005; Schaefer & Stobbe, 2006; Stevens *et al.*, 2006; Fraser *et al.*, 2007; Webster, Godin & Sherratt, 2015; Troscianko, Skelhorn & Stevens, 2017). The

same effect can be used to disguise features other than the outline by having highly salient false edges that run across different body parts, something Cott called ‘coincident disruptive coloration’. Again, this reduces detectability to both birds and humans (Cuthill & Szekely, 2009). Intersection of true edges is not even a prerequisite of effective disruptive coloration, as high contrast colour patches within the body’s edge can also conceal (Fig. 2; Stevens *et al.*, 2009). False edges can mask nearby true edges through sub-attentive mechanisms such as lateral inhibition and contour capture (Troscianko *et al.*, 2009).

Edge-disrupting camouflage may be also be favoured because, if particular types of coloration involve a feature that is consistent across prey (e.g. an uninterrupted outline), search image formation will be facilitated (Troscianko, Skelhorn & Stevens, 2018). However, there are a couple of caveats to the effectiveness of disruptive coloration. First, if the high contrast patches are themselves colours or patterns not found in the background, the lack of background matching imposes a cost. Certainly, in the tightly controlled circumstances of a visual search experiment for a specified target, humans rapidly learn that an unusual colour is a cue to target presence (Fraser *et al.*, 2007). However, even in the field, where birds are searching for multiple prey types, with other tasks to attend to, high contrast achieved through non-background-matching colours or tones reduces (but does not eliminate) disruptive coloration’s effectiveness (Schaefer & Stobbe, 2006; Stevens *et al.*, 2006), if only because conspicuousness of even unrecognisable shapes invites closer inspection. That said, as Cott (1940) argued, salient features may be detected pre-attentively but not recognised as part of an object worthy of inspection, an effect verified for humans with an eye-tracking experiment (Webster *et al.*, 2013).

The second caveat is that highly salient false edges can impose the same cost as highly salient colour patches if 'strong edges' are not found in the background. As such, disruptive coloration is likely to work best in environments which possess differently coloured objects with clearly defined edges; possessing colour patches that match different objects enhances the likelihood that each patch on the target segregates with a different background object rather than as a coherent whole (Espinosa & Cuthill, 2014). Having surfaces that appear to lie at different distances from the viewer (different depth planes) is also effective (Egan *et al.*, 2016), because surfaces that lie in different depth planes are less likely to 'belong together' than those in the same plane. Cott (1940), as Thayer (1909) before him, drew attention to what appear to be false depth cues in animal camouflage, something he called 'pictorial relief'.

Distraction marks

"When the surface of a fish, or of a factory, is covered with irregular patches of contrasted colours and tones, these patches tend to catch the eye of the observer and to draw his attention away from the shape which bears them" (Cott, 1940, p.49). These words appear near the opening of Cott's chapter on Disruptive Coloration, but modern accounts usually treat distraction of attention as a distinct process from the breaking up of shape and form (Stevens & Merilaita, 2009; Osorio & Cuthill, 2015; Merilaita, Scott-Samuel & Cuthill, 2017; Ruxton *et al.*, 2018). Distraction is the main tool of the magician, but bearing conspicuous marks on your own body would seem to carry the same cost as use of non-background-matching colours in disruptive coloration (see above). Visual search experiments with humans show that conspicuous marks like this are learnt and, as a result, increase detectability

(Troscianko *et al.*, 2013; Troscianko, Skelhorn & Stevens, 2018); field experiments with artificial prey show similar effects (Stevens *et al.*, 2008, 2013a). However, one aviary experiment with birds searching for artificial prey on patterned backgrounds has shown that conspicuous, non-background-matching marks can reduce predation rates (Dimitrova *et al.*, 2009). One possible resolution to these contradictory results is that, although ineffective if a mark is a unique cue to target presence, distraction by conspicuous marks could work if the latter are sometimes also found in the background (Osorio & Cuthill, 2015). It is also the case that the issues are muddied because the term distraction (or distractive) mark has been used in different ways, from Thayer (1909) onwards; see the discussion between Merilaita *et al.* (2013) and (Stevens *et al.*, 2013b), and in Ruxton *et al.* (2018).

Self-shadow concealment

Unless pressed flat to the substrate, illumination of an animal creates shading patterns different from those of the substrate, and the shading itself offers clues to the animal's 3D shape. Abbott Thayer, as an accomplished artist, recognised the importance of shape-from-shading for object recognition and, moreover, that strategic use of colour could obliterate those cues (Thayer, 1896). The entomologist, and ardent Darwinian, Edward Bagnall Poulton had earlier, and seemingly unbeknown to Thayer, proposed the same idea (Poulton, 1890). With light coming from above, a uniformly coloured animal would appear lighter on its top and in shade below, the gradient of reflected light revealing its presence and shape. However, if the animal was darker on top and lighter below, this *countershading* could nullify the shape-from-shading cues. Thayer saw the widespread taxonomic distribution of countershading as overwhelming evidence for camouflage through self-shadow

concealment; he called his paper “The law which underlies protective coloration” (Thayer, 1896).

Possession of two-tone coloration, with the darker side facing the light, is not evidence that it functions as self-shadow concealment (Rowland, 2009); careful modelling of the light field around animals shows that the pattern, and animal’s orientation, have to be quite closely matched to the illumination conditions (Penacchio *et al.*, 2015a, 2015c). However, comparative studies of some taxonomic groups show that the observed pattern of countershading fits what we’d expect if countershading is to nullify the shading created by the illumination. Those primates which largely walk on all fours have lighter bellies than backs, while primates that are more often in vertical poses, do not (Kamilar & Bradley, 2011). Ruminants living in open environments, and nearer the equator, have stronger countershading, in line with the stronger shadows found in these conditions (Allen *et al.*, 2012). One can even use this expected association between countershading and light environment to predict the habitats occupied by dinosaurs where the pigment distribution has been preserved (Vinther *et al.*, 2016; Smithwick *et al.*, 2017). However, there are other reasons for an animal to be darker on the side facing the light (Kiltie, 1988; Ruxton, Speed & Kelly, 2004). Both UV protection and thermoregulation predict uneven distribution of pigments, and modelling of the light field around animals shows that the predictions for pigment distribution in relation to these different functions are hard to separate (Penacchio *et al.*, 2015c). Such modelling also shows that orientation with respect to the sun is also predicted to be similar for these alternative functions (Penacchio *et al.*, 2015a). With these multiple alternative

functions for countershading, we need behavioural evidence that this coloration enhances concealment.

Field experiments with artificial caterpillars made of differently coloured dough have shown that countershading reduces predation rates compared to plain background-matching controls (Rowland *et al.*, 2007, 2008). This is direct evidence for a camouflage benefit ('upside-down' countershaded prey do not survive well, ruling out neophobia or aposematism as explanations). More convincing still are results, also with artificial prey in field experiments with avian predators, showing illumination dependence of the benefits of different patterns. Cuthill *et al.* (2016) used caterpillar-sized paper cylinders containing mealworm baits, printed with patterns predicted to be optimal when viewed by birds under diffuse versus direct illumination (based on the light-field models of Penacchio *et al.*, 2015c). Prey patterned with the diffuse-lighting optimum survived best in shade or on cloudy days; prey with the direct-lighting optimum survived best in in the open on sunny days. Human visual search experiments in computer-generated environments with different types of illumination, similarly show that countershaded 'caterpillar' targets are harder to find among similar, but flat, leaves, but only when the countershading is 'right' for the illumination (Penacchio *et al.*, 2015b; Penacchio, Harris & Lovell, 2017; Penacchio, Lovell & Harris, 2018). These experiments show that self-shadow concealment by countershading works, but under quite constrained conditions that depend on the illumination and the animal's orientation.

Although this section of the review is about concealment of form, it is important to recognise that there are also camouflage benefits of dorso-ventral differences in

pigmentation that are unrelated to concealment of 3D shape. First, if pigment-production has costs and the belly is rarely exposed, there is no need for pigmentation there (Ruxton, Speed & Kelly, 2004). Second, if background matching is the goal, different potential viewing positions can mean that different backgrounds have to be matched by the dorsum and ventrum. Aeroplanes in WW2 were often painted with camouflage on top and pale colours below, not to conceal shape but instead because the top is viewed from above against the ground, and the underside from below against the sky. The same has been argued for countershading in aquatic organisms, with dorso-ventral differences in pigmentation in the western rainbowfish (*Melanotaenia australis*) more consistent with background matching than obliteration of 3D shape cues (Kelley & Merilaita, 2015). Although a white belly cannot match the intensity of downwelling light (Penacchio *et al.*, 2015c), a range of pelagic fish species have independently evolved downward-facing photophores with bioluminescence that can be adjusted to match the downwelling light and diminish the fish's silhouette: counterillumination (Case *et al.*, 1977; McFall-Ngai, 1990; Harper & Case, 1999).

Preventing recognition

Many have drawn a distinction between camouflage by means of matching the general background and through mimicry of specific objects within the background. Poulton called the former 'general resemblance' and the latter 'special resemblance' (Poulton, 1890). The latter is now more commonly termed masquerade, following the influential review of Endler (1981). In that review, Endler sought not only to clarify the distinction between masquerade and background matching, but also that between

masquerade and other forms of ‘adaptive resemblance’ (Starrett, 1993), notably Batesian and Müllerian mimicry. What should or should not be called mimicry, and where and how to draw distinctions, has been a topic of intense debate for decades. The history of debate, and the complexity of the issues, is comprehensively reviewed by Quicke (2017). Here I summarise the key messages from this literature (see also the very accessible accounts by Stevens, 2016; Ruxton *et al.*, 2018).

There are two potentially defining differences between mimicry of a stone or dead leaf (examples of masquerade) and mimicry of a toxic butterfly (an example of Batesian mimicry). Neither involve the consequences for the predator. Even though classic Batesian mimicry involves resemblance to a toxic model, the consequences of consumption of which are potentially lethal, eating a twig rather than a twig-mimicking caterpillar is probably not very good for the predator either. At a minimum, both errors involve time and energy costs. A useful distinction must therefore lie elsewhere. First is the relationship between the (minimally) three parties involved: the two senders of information (model and mimic) and the receiver (Wickler, 1965). Endler (1981) highlighted the fact that when the signal receiver (say, a predator) attacks objects resembling a Batesian mimic (because it has learnt that some are undefended), this imposes selection on the model to ‘evolve away’ from the mimic (e.g. Kraemer, Serb & Adams, 2015). Instead, attacking a stone because of the possibility it is a tasty stone-mimic has no evolutionary consequences for the stone. Mimicry of bird droppings by some spiders and moth caterpillars (Liu *et al.*, 2014; Valkonen *et al.*, 2014; Suzuki & Sakurai, 2015), fulfils Endler’s criterion for masquerade, not Batesian mimicry, even though erroneous consumption of faeces could be harmful. Birds have not, as far as we know, evolved differently coloured or

shaped faeces as a result of mimicry by arachnids or insects. For models of masquerade that are living rather than inanimate or dead, there is plausibly a spectrum between masquerade and Batesian mimicry. When an insectivorous bird pecks a twig rather than a twig-mimicking caterpillar, there may be some damage to the plant and thus, in the limit, there is selection on the plant to avoid being mistaken for the caterpillar. However, the frequency of such attacks is likely to be low, the damage minimal, and the other selection forces on twig morphology so large, that twig-mimicry and its like are firmly at the masquerade end of that spectrum.

The second possible discriminator between masquerade and other forms of adaptive resemblance, including background matching, lies in the behaviour and cognition of the receiver (Skelhorn *et al.*, 2010b; Skelhorn & Rowe, 2016). The adaptive value of aposematism lies in the pairing a signal of unprofitability with the unprofitability itself, such that predators learn to avoid that signal (Mappes, Marples & Endler, 2005; Rojas, Valkonen & Nokelainen, 2015; Skelhorn, Halpin & Rowe, 2016; Skelhorn, Holmes & Rowe, 2016). Batesian mimics therefore benefit by being actively avoided, whereas masqueraders are ignored as irrelevant. The idea that masqueraders may be detected, but are ignored, lies behind the proposal that misclassification, rather than impaired detection, distinguishes masquerade from background matching and other forms of cryptic coloration (Endler, 1981, 1988, 1991; Skelhorn *et al.*, 2010b; Merilaita, Scott-Samuel & Cuthill, 2017; Ruxton *et al.*, 2018). For this reason, Caro and Allen (2017) classify masquerade as a signal (false information), whereas crypsis is not (absence of information). The thought experiment here is that an animal that relies on crypsis must be on the right background, but a masquerading animal could be completely visible on a mismatching background, but still

misclassified by a predator as ‘not food’. It is this difference that inspired Skelhorn and colleagues to perform a series of experiments where prior experience of what might or might not be food was manipulated (Skelhorn *et al.*, 2010a, 2010b; Skelhorn & Ruxton, 2010, 2011). It may appear surprising that it took 120 years, from Poulton’s illustrations of twig-mimicking caterpillars, for the first systematic experiments on the basis of masquerade to be performed, but this is probably because the benefit for a caterpillar of looking like a twig seems self-evident (“A stick is a stick and not worth eating”; Robinson, 1981). In fact, the mechanism is more subtle than it might at first appear.

In their first experiment, Skelhorn and colleagues pre-exposed naïve domestic chicks (*Gallus gallus domesticus*) to three types of environment: an empty arena, an arena with hawthorn branches, and an arena with hawthorn branches that had been bound with purple thread (Skelhorn *et al.*, 2010b). In test trials, they then introduced chicks to either one of two types of hawthorn-twig-mimicking caterpillars (*Opisthograptis luteolata* and *Selenia dentaria*) or a hawthorn twig. Birds which had had the opportunity to learn that twigs are not good to eat, showed a greater latency to attack, and more caution in handling, twig-mimicking caterpillars. Crucially, the birds whose prior experience of branches were of branches that, because of the purple thread, did not look like the caterpillars, responded to the caterpillars in a similar way to those with no prior experience of branches at all. This shows that the caterpillars had higher survival because they looked like objects that the birds had learnt were inedible, not because the caterpillars were not detected. In subsequent experiments, the benefits of twig-mimicry were lower when real twigs were simultaneously present, and by inference direct comparison was possible (Skelhorn & Ruxton,

2010), and also lower when prey were found in a context in which the model had not previously been encountered (Skelhorn & Ruxton, 2011).

Skelhorn and colleagues' experiments show the importance of predator learning for the success of masquerade, but there will be cases where the distinction between camouflage through masquerade and through crypsis is less clear-cut. The biological literature tends to treat detection and recognition as serial processes, with objects segmented from the background and then recognised or not. However, it is now known that familiarity with the background improves search for unfamiliar targets (Chen & Hegdé, 2010), and that learnt properties of textures affect the efficiency of texture segmentation (Meinecke & Meisel, 2014; Becker, Smith & Schenk, 2017). If learning affects which features in the background are selected, pre-attentively, for inspection or not, then crypsis and masquerade may not always be easily separable using experiments such as those of Skelhorn and colleagues. A twig-mimic may be passed by because the predator has learnt that twigs are not food (masquerade) or because it has learnt that the features of twigs are part of the background. Such features therefore do not reach the threshold for selective attention and failed detection is the result; this now looks like crypsis.

Whether 'twig' is an object category confusable with 'food', as the definition of masquerade assumes, is itself a cognitive construct that needs to be established empirically, and will not apply in simpler organisms. In Lettvin *et al.*'s classic demonstration of 'bug detector' neurons in the frog, firing was prompted by a dark moving stimulus the size of an insect prey (Lettvin *et al.*, 1959). It is a matched filter, such that detection and recognition are one and the same process. A top-down

process that affects object detection in even cognitively complex organisms has already been discussed: search image formation (Pietrewicz & Kamil, 1979; Plaisted & Mackintosh, 1995; Langley, 1996). If, through selective attention, what you are looking for affects your probability of detecting it then, necessarily, detection and recognition are not readily separable nor, perhaps, is it useful to do so. This is not an argument against the value of attempting to isolate where, in the process of perception, cognition and behavioural output, different camouflage strategies have their influence; it is just a warning that this will not always be straightforward.

Constraints on camouflage

It is clear that background matching and, in the case of masquerade, the need for the model to have been encountered, places constraints on habitat choice. Whether these can be ameliorated by compromise camouflage has already been discussed. It has often been proposed that disruptive coloration reduces the severity of the constraint on background choice but it has not, to my knowledge, been demonstrated that disruptively coloured animals have broader niches, in terms of background types, than background-matchers. The importance of differential blending means that disruptive coloration is not totally independent of background matching (Sherratt, Rashed & Beatty, 2005), so the proposition that disruptive coloration reduces the constraints on habitat choice should be tested. Below, I discuss some other important constraints on camouflage.

Size

Defences which putatively rely on intimidation, like eyespots, are ineffective on animals with smaller body sizes (Hossie *et al.*, 2015). Furthermore, the switch between camouflage and aposematism can be size dependent (Valkonen *et al.*, 2014). However, I know of no systematic investigation of whether the type of camouflage seen varies with body size. All things being equal, one might think it harder to hide a large animal than a small one but, if camouflage is favoured, then factors other than absolute size should be more important for camouflage involving background matching and disruptive coloration. Body size in relation to the size of colour patches in the substrate determines whether the latter can be considered a homogeneous texture or a patchwork of different backgrounds (Endler, 1978, 1990, 2012; Bond & Kamil, 2006). The distance at which a target could in principle be detected, as affected by habitat type and the spatial acuity of the viewer, will similarly affect how fine- or coarse-grained the patterns need to be to be effective (Endler, 1978, 1990; Caves, Brandley & Johnsen, 2018). This is presumably why military vehicles rarely bear camouflage as detailed as that seen on uniforms; the latter may need to be effective at a few metres while the former needs only work from afar.

Absolute size should constrain which objects could be mimicked in masquerade, assuming that the viewer uses absolute size as a criterion in discrimination. However, we should not take the latter as a given, because some other types of mimicry seem to be effective without a close size-match. The effectiveness against avian predators of snake-mimicry in certain caterpillars is enhanced by a match in shape and posture, in addition to paired eye-like markings (Hossie & Sherratt, 2013; 2014); this leaves little doubt that the snake-like appearance is more than a

resemblance imagined by humans. However, the caterpillars are much smaller than the snakes being mimicked, so either caterpillar-sized (e.g. baby) snakes are considered a threat by birds or absolute size is not taken into account by the avian predators involved. This deserves further study, because it is surprising.

Shape

As discussed earlier, having contours unlike those found in the background increases detectability and, if detected, shape is often the primary cue to identity. We have already seen how disruptive coloration at the body's edge can reduce the signal of shape. The detectability of a characteristic outline can also be reduced by varying posture and orientation (Webster *et al.*, 2009). The extent to which shape itself can be modified by selection for reduced detectability will depend on trade-offs with mechanical effects, most obviously in locomotion. The trailing edge of the wings of butterflies such as the comma (*Polygonia c-album*) is highly irregular, not only enhancing similarity to a dead leaf but also departing from the common butterfly template; but the leading edges of the wings are of a typical aerofoil shape. Cott (1940, p. 96) called the former "irregular marginal form".

Symmetry

As well as a symmetrical outline providing shape cues, symmetrical patterning on a surface increases detectability to birds as well as humans (Cuthill, Hiby & Lloyd, 2006). Although one might think that the high contrast and strong (false) edges of disruptive coloration might be more salient in symmetry than a simple background-matching pattern, the cost of symmetry in terms of detectability appear similar (Cuthill *et al.*, 2006). Symmetrical coloration is not an issue for masquerading

animals if the model is symmetrical, or for animals where both sides of the body are rarely seen at once. It nevertheless remains a puzzle that even otherwise highly cryptic moths, where both wings are seen in plan view, have symmetrical colour patterns. If the reasons lie in developmental constraints, then the costs of bearing symmetrical camouflage needs to be offset by other means, such as posture (Cuthill, Hiby & Lloyd, 2006; Cuthill *et al.*, 2006).

Oriented textures

If the background has an oriented texture, such as the vertical grain of bark on trees such as oak, then a background-matching animal has to orient such that its texture matches (Sargent, 1966; Kang *et al.*, 2012, 2014b; Barnett *et al.*, 2016). This demands the ability to detect the background texture, not necessarily visually because tactile cues may suffice, and orient appropriately. An elegant series of experiments by Kang and colleagues followed Sargent's classic work to show exactly how this is done in a moth that matches textured bark, including post-landing readjustments to improve concealment (Sargent, 1966; Kang *et al.*, 2012, 2013, 2014a, 2014b).

Movement

Stone-mimicry by certain plants is compatible with their sedentary lifestyle (Lev-Yadun, 2014; Niu, Sun & Stevens, 2018), but most animals have to move at some point in their lives. Correlated motion of primitive features is one of the most powerful and rapid cues for figure-ground segmentation (Regan & Beverley, 1984; McLeod, Driver & Crisp, 1988), even when the object matches the background closely (Ioannou & Krause, 2009; Stevens *et al.*, 2011; Hall *et al.*, 2013). The fact that

motion breaks camouflage is therefore a significant constraint on activity, and the trade-off between the camouflage-breaking costs of motion and the benefits of being able to move is a major factor determining which anti-predator defences evolve (Edmunds, 1974; Ruxton *et al.*, 2018). There are, however, some mitigating factors (Cuthill, Matchette & Scott-Samuel, 2019). Motion of background objects such as foliage (Ord *et al.*, 2007; Peters, Hemmi & Zeil, 2007; New & Peters, 2010) or rapidly changing illumination (Matchette, Cuthill & Scott-Samuel, 2018) can both mask movement. Moving as part of a group, as well as the well-recognised benefits of aggregation *per se* (Krause & Ruxton, 2002), can be safer because matching both background and group-mates reduces the efficiency with which predators can single out one animal for attack (Hall *et al.*, 2013; Hogan, Cuthill & Scott-Samuel, 2016, 2017; Hogan, Scott-Samuel & Cuthill, 2016; Hall *et al.*, 2017).

Conclusions

Camouflage comprises an array of mechanisms that impede accurate sensory processing. Some forms of camouflage defeat accurate classification at a very early stage: if the light coming from a target generates exactly the same spatiotemporal distribution of simple visual features, such as the orientation and spatial frequency of contrasts in lightness or hue, as those generated by light from the background, then there is no information with which to separate target from background at this, or any subsequent, stage of visual processing. Conversely, a stick insect on a contrasting background has readily detectable features, so its survival depends on a misclassification by a predator at the stage of whole-object recognition (Skelhorn *et al.*, 2010b). Motion similar to the mimicked object reduces discriminability (Bian,

Elgar & Peters, 2016; Cuthill, Matchette & Scott-Samuel, 2019); dissimilar motion enhances discriminability. In some cases, it is not a minimisation of signal that is effective, but an increase in noise, such as the creation of false edges in disruptive coloration. Another example, although not 'camouflage' as such, is the effect of the environment itself on detectability. It is harder to find targets when the illumination is complex (Matchette, Cuthill & Scott-Samuel, 2018), and on more complex backgrounds (Merilaita, 2003; Dimitrova & Merilaita, 2010; Xiao & Cuthill, 2016). There is some evidence that the latter affects background choice in lab experiments on fish (Kjernsmo & Merilaita, 2012), but whether this is widespread in nature deserves investigation now that models exist to quantify background complexity (Xiao & Cuthill, 2016).

A related issue that is an exciting avenue for research is how animals that choose substrates or change appearance assess the relevant features of the background (see discussion in Stevens & Ruxton, 2019), given that their vision may differ markedly from that of the species they are hiding from. The best understood system here is the cuttlefish, because the changing appearance of its skin tells you directly how it perceives its background (Hanlon & Messenger, 2018). For example, strong edges in its visual field will cause it to produce disruptive patterns with false relief, excellent camouflage on a stony background (Zylinski, Osorio & Shohet, 2009). How individual quail "know" the pattern on the eggs they will lay, and accordingly select appropriate nest scrapes, is rather more mysterious (Lovell *et al.*, 2013) and an example of the challenge facing vision scientists unlucky enough not to work on cephalopods.

So far, the only mention of camouflage in non-animals has been a passing comment about stone-mimicry in certain plants (Lev-Yadun, 2014; Niu, Sun & Stevens, 2018). All the principles applied to, and illustrated with, animal camouflage should be applicable to other taxa, and some pioneers have started to mine what will be a rich vein of research. Examples of background matching, disruptive coloration and masquerade have been advanced (Lev-Yadun *et al.*, 2004; Lev-Yadun, 2006, 2014; Niu *et al.*, 2017; Kjernsmo *et al.*, 2018), along with parallels of many other defensive uses of coloration more commonly associated with animals (Schaefer & Schmidt, 2004; Ruxton & Schaefer, 2011; Caro & Allen, 2017). I feel that plant camouflage research is in the position that the field, for animals, was 20 years ago; there is an array of highly plausible examples based on deep natural history knowledge but, as yet, few rigorous experimental investigations of these. The same can be said of camouflage in other sensory modalities, where examples of acoustic and olfactory crypsis are rare surely only because of, as yet, limited research on the topic (Ruxton, 2009). When it comes to chemical camouflage, it is ubiquitous in micro-organisms, but is not usually described as such. A successful parasite or pathogen must avoid detection and recognition of cell-surface antigens by an immune system. These are the outer layers of the survivability onion (Figure 1).

Camouflage research, as with the study of biological colour more generally, has evolved rapidly in the last decade because it provides a common research focus for diverse fields with complementary questions and techniques (Cuthill *et al.*, 2017). Moreover that interdisciplinarity is necessary. One cannot understand many of the features of animal camouflage – for example enhanced edges to disruptive patterns – without appreciating the sensory and cognitive mechanisms of the viewer that the

patterns have evolved to deceive. One cannot understand the constraints on camouflage – such as symmetry – without a knowledge of the developmental genetics of pigmentation. The next phase of camouflage research is likely to start to apply interdisciplinary insights and techniques to address broader questions in time and space. One recent example is the use of palaeocolour to infer habitat type and predator visual perception in extinct species (Vinther, 2015; Vinther *et al.*, 2016; Smithwick *et al.*, 2017). Another is the broad-scale analysis of the effect of climate change on selection for the ability to change colour seasonally, as seems to be happening currently in several high-latitude mammal species (Mills *et al.*, 2013, 2018; Pedersen, Odden & Pedersen, 2017). The insights of the Victorian and early 20th century naturalists, like Poulton and Cott, and artists like Thayer, were profound and inspiring, but only now is a deep understanding of animal camouflage finally emerging.

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Figures

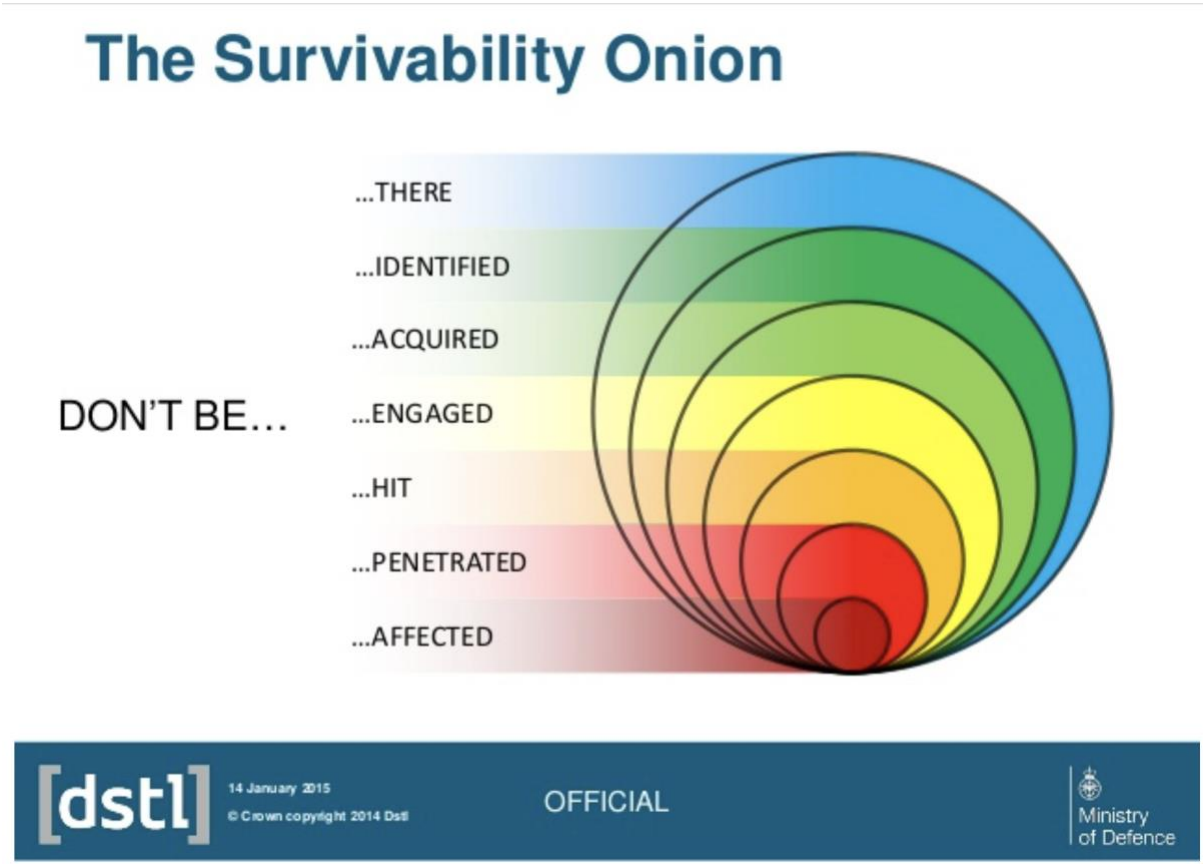

Figure 1. The Survivability Onion. Slide 17, 13 January 2015 Enduring Challenge Briefings for the Centre for Defence Enterprise, UK Ministry of Defence © Crown Copyright 2015. Reproduced under the terms of the Open Government Licence http://www.nationalarchives.gov.uk/doc/open-government-licence/version/3/.

Figure 2. Different camouflage strategies that a frog might employ for a forest-floor background. Left to right: background matching (a frog-shaped sample of the background), edge disruption (high contrast patches breaking up the body's edge), surface disruption (breaking up the body's surface with high contrast patches that are perceived as distinct objects, so not part of a recognisable animal), surface disruption with edge enhancement (edge disruption with edge enhancement is also possible), and masquerade (mimicry of a leaf). Forest floor photo from French Guiana, © C. Michalis 2014.

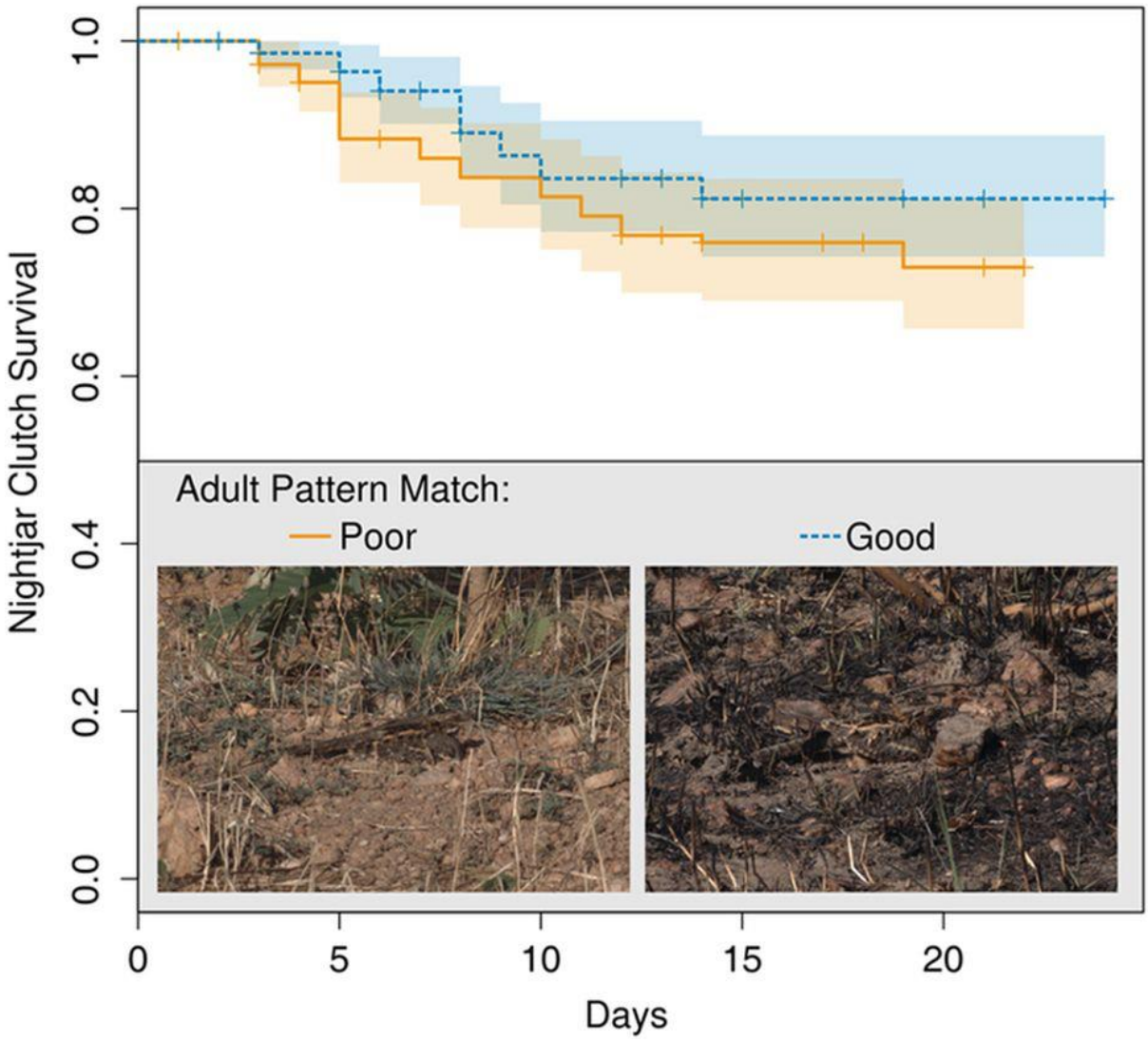

Figure 3. Figure 3 from Troscianko *et al.* (2016), showing the survival of nightjar clutches as a function of time and whether the incubating parent had above (blue) or below (orange) the median match with the immediate background (shaded areas are 95% confidence intervals). The photographs show examples of adults with poor (left) and good (right) matches to their backgrounds. Reproduced under Creative Commons Attribution 4.0 Licence https://creativecommons.org/licenses/by/4.0/legalcode.